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BOTRYTIS AND SCLEROTINIA: THEIR RELATION TO CERTAIN PLANT DISEASES AND TO EACH OTHER.

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(WITH PLATES XXV–XXVII AND THREE FIGURES)

IN connection with the work of the Hatch Experiment Station of the Massachusetts Agricultural College, a disease of hothouse lettuce has been under investigation for several years. The practical results of this investigation will appear in a bulletin of the station. It is the purpose of the present article to present some results of this study which seem to have a value beyond that of their practical relation to the lettuce disease, and to discuss these results, together with some obtained by other investigators, with a view to clearing up some unsettled points in the life history of certain fungi.

The question of the relation of certain species of the Polyactis section of the genus Botrytis to certain species of Sclerotinia is no new one. The literature of plant diseases, especially in Europe, abounds in descriptions and discussions of cases of plant diseases where one or the other or both of these forms appeared, and considerable difference of opinion has resulted as to their real relations to the disease and to each other. In this contention are involved principally two species of Sclerotinia, namely: *S. Fuckeliana* De By. and *S. Libertiana* Fckl., and one species of Botrytis, *B. cinerea* Pers. (*B. vulgaris* Fr., and numerous other synonyms). Largely on the authority of De Bary,

Botrytis cinerea has been considered the conidial form of *Sclerotinia Fuckeliana*, and the existence of any such conidial form of *S. Libertiana* has been denied. Some investigators have disputed this, however, claiming that in certain cases *Botrytis cinerea* has developed in undoubted connection with *Sclerotinia Libertiana*, thus casting doubts on the distinctness of *S. Fuckeliana*. The present article contains a description of the investigation of the above mentioned lettuce disease, in so far as it bears on this subject, together with some other observations made by the writer, and abstracts of descriptions of several similar diseases investigated by others.

1. The lettuce disease.

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In the Report of the Massachusetts Experiment Station for

1891 Humphrey (1) described a disease of greenhouse lettuce, from which the following is an abstract:

The trouble ordinarily appears first upon the stem of the plant, about at the surface of the soil. Here may be seen at first a soft, dark, decayed spot, which rapidly spreads, penetrating the stem and involving next the bases of the lower leaves. The latter, being thus cut off from the plant by the decay of their bases, usually dry up. With the further progress of the decay the center of the head, with the tender inner leaves, becomes attacked, and soon collapses into a fetid, slimy mass. In the decaying tissue one can often recognize fungus threads, and if they are left undisturbed, there appear on the decayed remains the fruiting threads and spores of a fungus; always the same. . . . . The fungus in question is one of the imperfect forms known as Botrytis or Polyactis. . . . . In its development, so far as observed, and in the details of its structure, this fungus appears to agree with the form known as *Botrytis* (*Polyactis*) *vulgaris* Fr.; and is with little doubt the conidial stage of some sclerotium-producing Peziza (Sclerotinia).

Since the above was written the lettuce-forcing industry in the vicinity of Boston has largely increased, and forms today one of the most important agricultural industries in the state. Diseases of the crop have naturally increased proportionally. It is evident that the trouble described by Humphrey covers what is now generally known in the lettuce district as the "drop," and probably also more or less of another disease distinguished by the growers as "black root." The "drop" is the worst obstacle to lettuce growing in the Boston district. Its general nature is described in the quotation from Humphrey. Plants growing finely and approaching maturity suddenly collapse, the stem at the surface of the ground and the bases of the leaves are found to be rotted, and in a day or two the plant is completely gone. Plants afflicted with the real "drop" never recover. In most of these sudden cases, however, no black spot appears on the stem as described by Humphrey, nor does any external change in appearance take place except that a white, mould-like fungus mycelium usually appears and grows vigorously upon the surrounding soil. This Humphrey does not mention, though it seems probable that he would have done so if it had occurred in the cases observed by him, as it is very striking. Careful study of these diseases show that many cases of "black root" come

closer to Humphrey's description. This trouble appears to start in some injury to the plant, such as the breaking off of a leaf, or where the plants grow poorly and the outer leaves die off. Starting in some such way a fungus growth develops which gradually works down into the stem on the side from which it started, producing a black, decayed spot, just as described by Humphrey. A growth of Botrytis appears on the affected parts, but the vigorous growth on the soil does not appear. The ultimate fate of such plants depends largely on the management of the greenhouse. If the soil is kept dry and the temperature low no great loss results, but should a period of high temperature and considerable moisture occur the plants soon "drop" in the characteristic manner. A trouble of this sort appears to be common wherever hothouse lettuce is grown. It has generally been ascribed to *Botrytis vulgaris*, largely on Humphrey's authority, and the idea appears to be general that it can be held in check by proper handling of water and ventilation. Thus Humphrey says:

> It is evident that the thorough and careful culture and vigilant supervision of the plants are essential to the control of the disease in question . . . . with a crop well nourished and well cared for one may legitimately expect practical freedom from loss by rotting.

The "lettuce rot" described by Jones (2) does not appear to be the "drop," although ascribed to *Botrytis vulgaris*. The trouble described by Taft (3) as caused by *B. vulgaris* may include the "drop," but the name "mildew" is ill-chosen. Galloway (4), referring to the Boston soil, says:

> Wet rot of the lower leaves and rotting of the stems and consequent wilting of the plant are seldom troublesome in this soil if properly handled, because the surface is at all times comparatively dry. Wet rot is produced by *Botrytis vulgaris*.

Bailey (6) has the same idea when he says:

> This lettuce rot is due to a fungus (*Botrytis vulgaris*) which lives upon decaying matter on the soil, but when the house is kept too warm and damp, and the lettuce becomes flabby, it invades the plant and causes irreparable damage. There is no remedy, but if the soil is sandy and "sweet" and the

house properly managed as to moisture and temperature, and top dressings of manure are avoided, the disease need not be feared.

Bailey's illustration shows a typical case of "drop." If these statements are to be believed the condition of affairs in many lettuce houses about Boston can but reflect seriously on the skill of their owners. The disease is there and in abundance, to all appearances the same trouble as described by Humphrey, Galloway, and Bailey. In some houses it is much worse than in others but the fact is undeniable that even in the houses of some of the best growers, men who possess a practical knowledge of their special crop second to none, the disease is almost unchecked. Evidently, therefore, *Botrytis vulgaris* is a more serious parasite than is generally supposed, or else some other organism or agency is at work, producing a similar effect.

The first cases of the disease examined by the writer agreed very well with Humphrey's description. The plants were completely collapsed and the stems and bases of the leaves soft and rotten. The affected tissue was filled with a vigorous mycelium (*fig. 51*). This mycelium was composed of large, branching, septate, hyaline filaments, filled with granular protoplasm, but with numerous vacuoles in the older portions. The larger filaments averaged about 13μ in diameter. On the borders of affected tissue filaments could be seen advancing (*fig. 50*). When placed in a moist chamber over night, the plants became covered in the affected parts with a vigorous growth of the conidial form, *Botrytis vulgaris* Fr. This growth, to all appearances, originated directly in the parasitic mycelium which had destroyed the plant. The conidiophores developed from the interior filaments (*figs. 13–17*). *Fig. 18* shows the development of the branches, and *figs. 1* and *2* represent a typical conidiophore of this species. The peculiar branching forms known as "organs of attachment" (*figs. 19–26*) were also abundantly produced from the mycelium on affected plants and in cultures, which could readily be made on prune juice, prune bread, prune gelatine or agar, boiled fruits or vegetables, or almost any nutrient substance. Contrary to Humphrey's results, sclerotia

were produced abundantly on affected plants and in cultures. These were very small and insignificant, but numerous in every case.

Humphrey's conclusions that the disease is caused by *Botrytis vulgaris* appears to have been generally accepted by all who have written concerning this disease. It is very probable that in some of the citations given above the disease was not the real stem rot or "drop," but simply a case of Botrytis on the leaves, as often occurs on all kinds of plants when growing poorly or under unfavorable conditions. But in many of the references it is evident that the typical stem rot was found and ascribed to Botrytis. In no case was any extended investigation made. Early in the writer's study of this disease it became evident that whatever the cause might be, many cases occurred in which no Botrytis could be found, although otherwise the disease was very typical. Extended observation of a very large amount and variety of material from various sources has shown the existence of what may be called three forms of the typical disease. This excludes some other lettuce troubles of a more or less similar nature.

THE BOTRYTIS TYPE.

This form of the disease has already been described in a general way. It should be clearly distinguished from cases where Botrytis grows locally, more or less as a saprophyte, or even as a true parasite, upon the outer leaves. The rotting of the stem and collapse of the leaves and head is the characteristic of this and all types of the real "drop." *Botrytis vulgaris* is well known as one of the fungi, though not, perhaps, the most common, which cause the death of young seedlings and cuttings by what is known as "damping off," a trouble entirely similar to the "drop" in its effect, being a rotting of the stem at the surface of the ground. The principal difference between "damping off" and "drop" from a practical standpoint is in the age of the plants affected. "Damping off" of lettuce seedlings is common and may often be traced to Botrytis. It would not

seem remarkable, therefore, for so similar a disease as the "drop" to be caused by the same fungus. But of course the occurrence of this so common species upon affected plants comes far from proving it to be the parasite, and especially since many cases of the typical disease occur where no trace whatever of this fungus, or at least of its conidial form, can be found, Humphrey's conclusions cannot be accepted without further and more definite proof. The most convincing case in this respect seen by the writer was that of a crop of lettuce grown in one of the station greenhouses in the winter of 1898–9. The "drop" had been introduced into this house for purposes of study in 1897 and had been abundant in each crop since then. In no case, however, had any Botrytis appeared. Meantime, a method of treatment had been developed by which this no-botrytis type of the disease was completely held in check. The treatment consisted in sterilizing the soil by means of steam, and crop after crop was grown, with or without the disease at will. When this crop was set out the plants were overgrown and "spindling," having been too long in the flats. Consequently the outer leaves died off and the plants received a severe set back. Added to this the house was not properly ventilated and on several occasions the temperature was much too high. Soon after being set out the plants began to "drop," and in a few weeks the majority of them, in treated and untreated soil alike, were gone. Affected plants showed a mycelium in the stem indistinguishable from that in all other cases. Organs of attachment occurred as usual. Botrytis was abundant on every plant, especially when kept over night in a moist chamber. No mycelium was visible upon the surface of affected plants nor did it spread to the surrounding soil, and it could not be seen that the disease spread from plant to plant. The leaves were scarcely or not at all affected except at the very base and the rotting was almost entirely confined to the stem, the rest of the plant drying up. There is no reason to doubt that these plants were affected primarily with *Botrytis vulgaris*, originating presumably from conidia in the air, and such is believed to have been the case. It appeared to be essentially a

case of belated "damping off," made possible by the weakened condition of the plants.

Cultures made from affected tissue from these plants and from the Botrytis conidia gave similar results. A rather scanty mycelium developed, bearing numerous organs of attachment and but few conidia. Often no spores developed until after several weeks, even in cultures made directly from conidia. Compared with cultures made from ordinary saprophytic *Botrytis vulgaris*, these seemed to show that as the fungus takes on a parasitic nature it produces fewer conidia and more organs of attachment, though it is extremely variable and uncertain in these respects. Sclerotia were sparingly produced in almost all cultures made from this material. These appeared first as reddish, blister-like elevations in the substratum, gradually becoming black and hard. They were mostly longer than broad, thin, firmly attached to the substratum and inseparable from it. *Text fig. 1 f* shows some of these sclerotia grown on gelatine, portions of which are still attached to them. The photograph does not bring out clearly the size and form of the single specimens, as it is impossible to separate them cleanly. Thus, *text fig. 1 f*^{a} is a piece of gelatine having on its surface two long, thin, narrow sclerotia lying parallel to one another, while f^{b} consists of several sclerotia with more or less gelatine. *Fig. 44* also represents some of these forms, but fails to bring out their thinness. If placed in wet sand soon after being formed these sclerotia produced an abundant crop of Botrytis conidiophores and conidia. The ability to produce conidia appeared to be lost with age, and after a few months drying the development was largely of mycelium, though this was rather scanty.

In order to determine still more fully the relation of Botrytis to the lettuce disease some investigations were made along the line of infection experiments. Humphrey reports such to have been unsuccessful. Experiments on early mature lettuce plants gave the following results.

1. Pieces of affected plants buried in the soil beside healthy plants generally produced the disease.

2. Diseased plants from the lot just described, which appeared to have a pure Botrytis disease, did not have this effect.
3. Water containing abundant conidia poured down into the head produced no effect.
4. The same result was obtained when the leaf stalks were

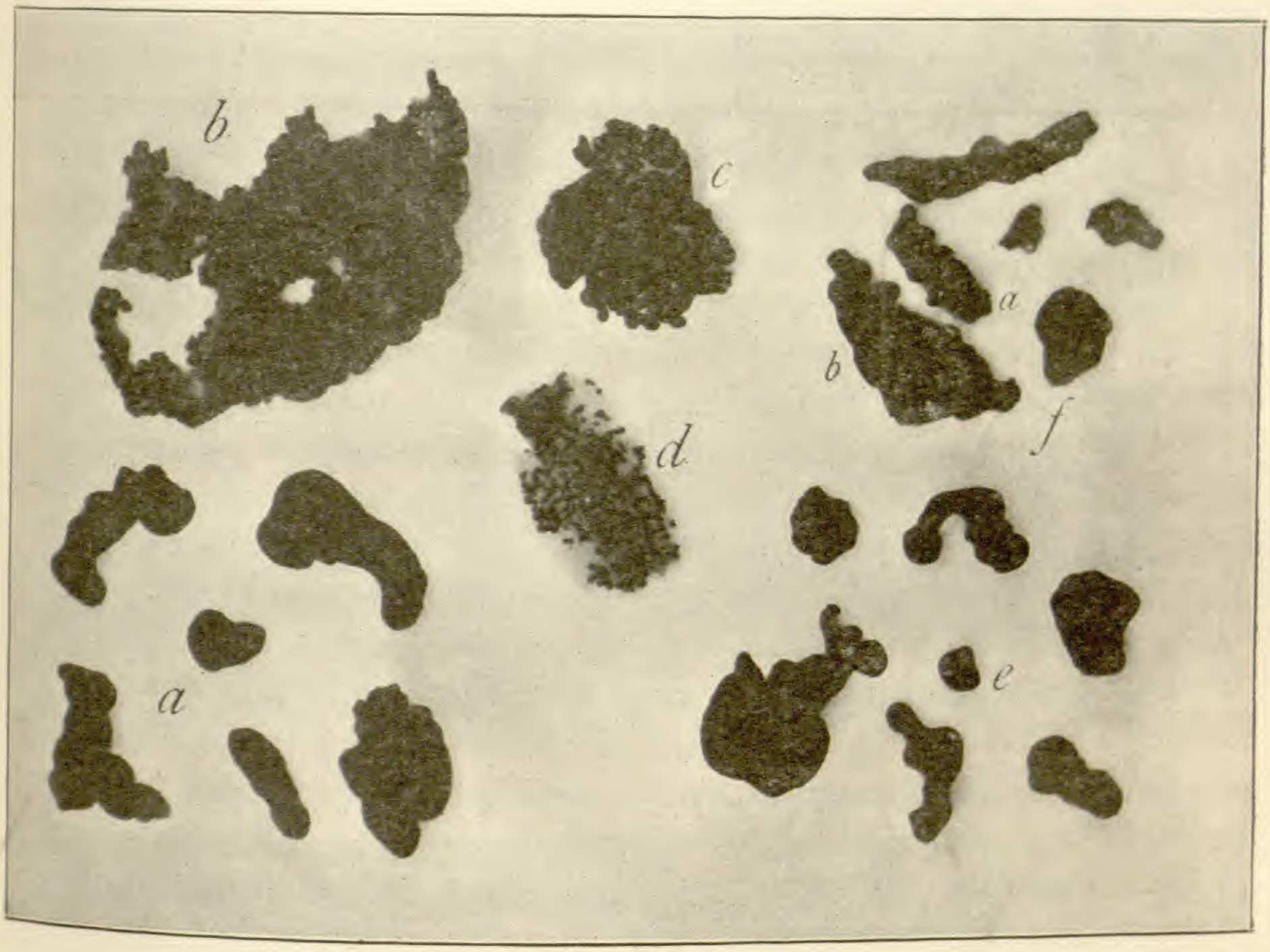

FIG. 1.—*a*, sclerotia of *Sclerotinia Libertiana*: *b*, *c*, sclerotial crust of lettuce fungus; *d*, small sclerotia from lettuce fungus; *e*, sclerotia of *S. Libertiana* from alfalfa; *f*, sclerotia of *Botrytis cinerea*.

cut into so that the conidia came into contact with wounded tissue.

5. Conidia dusted all over plants in great abundance had no effect.
6. Plants treated as in 5 but covered with a bell jar became affected in the leaves, which gradually died and rotted away, but the stem was unaffected and no typical "drop" resulted.

7. When the stem was cut into at the surface of the ground and mycelium and conidia inserted, no effect was apparent.

From these experiments it appears that the typical "drop" cannot be produced from Botrytis conidia in vigorous lettuce plants under ordinary conditions.

The following experiments were made with lettuce seedlings. A dish of soil was sterilized and then thoroughly inoculated with fresh Botrytis conidia. Lettuce seed was then sown. The plants came up well and remained entirely unaffected. The soil was then sprinkled heavily with conidia among the seedlings, with the result that one "damped off." The stem was permeated with a mycelium entirely similar in appearance to that found in the "drop." A portion of this is shown in *fig. 27* (cf. *fig. 51*).

The dish was then covered with a bell jar and kept very moist, but no more plants were affected. Prune juice containing conidia was then poured amongst the plants and the dish kept in the open air. "Damping" at once set in, and in a few days all the plants succumbed in the characteristic manner. Cultures made from these plants on prune and turnip showed the parasitic peculiarities of Botrytis already referred to. A considerable mycelium was produced at first but very few conidia until later. Raw turnip was readily attacked and caused to rot. This experiment corroborates Kissling's[1] results in regard to *Botrytis cinerea* that conidia are unable to, or at least do not readily, attack living tissue except after previous saprophytic nourishment.

In respect to the general question as to the relation of Botrytis to the "drop," these results seem to show that the disease is not produced in vigorous plants by direct infection from conidia in the air or soil, although in the case described above, where the vitality of the plants was very low, such appears to have been the case. The same conclusion may be deduced from the usually sucessful result of sterilizing the soil. There appears to be no doubt that the cases where "black root" develops into the "drop" belong to this form of the disease, and also the trouble which Humphrey, Galloway, and Bailey had in mind in referring

[1] Hedwigia **28**: 227. 1889.

to its treatment. Were this the only form to occur it would cause little trouble in the Boston district, as it is almost unknown there except for an occasional case of "black root."

THE NO-BOTRYTIS TYPE.

Among all the cases of the disease examined by the writer, those in which Botrytis appeared have been by far the exception. In the type of the disease most prevalent in Massachusetts no conidial form whatever can be found. In its general effect the disease is entirely similar to that already described and indistinguishable from it. Affected plants wilt and collapse and in a few days are entirely destroyed. The usual mycelium is found in the stem. It is also usual to find an abundant, white, woolly mycelium proceeding from affected plants to the surrounding soil where it flourishes luxuriantly for a time, often spreading to and attacking adjacent plants. In fact it is evident that whatever form of reproduction this fungus may possess its principal mode of spreading in the greenhouse is by growth in the soil. Wherever one plant is attacked the neighboring ones almost always follow, and the mycelium grows luxuriantly upon the soil, extending from plant to plant. On coming into contact with a healthy leaf it spreads over the surface, forming numerous organs of attachment (*fig. 31*). *Fig. 29* shows in cross section the result of this, the epidermis breaking down and the filaments penetrating and destroying the leaf. Sclerotia are formed in considerable abundance on affected plants, especially on the stem and beneath the leaves, but they are very small and easily overlooked in the soil. Cultures are easily made with bits of affected tissue or mycelium, and hundreds have been made in this way with no sign of Botrytis. Such cultures produce a considerable mycelium, more abundant on bread than on gelatine, and very numerous sclerotia. This mycelium is composed of filaments indistinguishable from those in the botrytis form. Organs of attachment are numerous and entirely similar. The sclerotia are very small, mostly about the size of a pin head. Some are a little larger, but thin and irregular in shape, while often a sort

of black sclerotial crust is formed, an inch or more in diameter, but not much thicker than paper. *Fig. 42* and *text fig. 1 d* show the small sclerotia of this type, and the crust-like growth is shown by *text fig. 1 b* and *c*, and by *fig. 43*. A clear distinction can be seen between the formation of sclerotia in this and in the botrytis form. Here they first appear as white specks in the mycelium, gradually becoming black and hard. They are not as long as those of the other form, and lack entirely the very characteristic blister-like connection with the substratum, being entirely distinct from it and imbedded in the mycelium. They are also produced much more abundantly. Many trials were made to obtain further development from these sclerotia. When placed on moist sand they usually produced a growth of mycelium, more copious from old specimens than fresh ones. Old dry material a year old grows luxuriantly when kept moist for a few days, producing much more mycelium than the Botrytis sclerotia. What might be called secondary sclerotia are also produced on such growths. On the surface of clean sand, on moist filter paper, or even on the bare bottom of a glass dish, when kept covered and moist, the mycelium coming from a sclerotium produces often a considerable number of smaller ones. The same result is often seen when a piece of affected tissue is placed in a moist chamber (*fig. 45*); and upon the surface of the soil about, and especially beneath the leaves of the affected plants, such secondary sclerotia are commonly produced. Being so small, however, they are difficult to distinguish in the latter case. Other than this no development has been obtained from these sclerotia except in one case. One of the largest specimens, about 3^{mm} in diameter, after being in the sand for some time, threw up a slender stalk (*fig. 35*). This reached a height of nearly 1^{cm}, but then withered and faded away without attaining any farther development.

Since no reproductive structures of this form could be obtained, infection experiments were only possible by using diseased tissue or masses of mycelium as infective material. Such experiments were almost invariably successful. Using plants

which showed this type of the disease in its purest form, or cultures made from them, it was found that when bits of diseased tissue were buried in the soil beside healthy plants, or inserted in cuts in the stem, the disease was at once produced. It was further found that if affected plants or portions of them were buried in a flower pot and lettuce plants set in, the latter would soon begin to die off and all eventually succumb, the mycelium soon appearing upon the surface of the soil in the characteristic manner. With sclerotia, pure mycelium, or pieces of sclerotia, the same results are obtained. In none of the experiments were the plants covered or placed under any conditions different from those of ordinary greenhouse culture. These results show plainly that this species or form is an active parasite, capable of causing the disease in the most vigorous plants at any age, but at the same time able to flourish under purely saprophytic conditions. It is likewise able to reproduce itself from year to year indefinitely by purely vegetative development, forming freely, either as a saprophyte or parasite, sclerotia which are able to survive all ordinary conditions[2] and produce the fungus anew. It would seem, in fact, that this is the only method of reproduction of this form. The results of sterilizing the soil have been already alluded to. It was found that when not less than three inches of the surface soil had been steam sterilized not a plant was affected, even in the worst infested beds. The only exception to this was the one crop where the pure botrytis type occurred. Plainly, therefore, the no-botrytis form depends very largely, if not entirely, upon saprophytic growth in the soil and the sclerotial resting stage for the continuance of its existence.

THE LARGE SCLEROTIA TYPE.

In a lot of lettuce plants sent by a gardener in eastern Massachusetts a third type of the "drop" was found. In this case the general nature of the disease was typical, and the parasitic

[2] Many results that relate to the biology of these forms are omitted here as they do not bear on the present subject.

mycelium indistinguishable from that found in other cases. No Botrytis appeared. The peculiarity of this form was that the sclerotia which were rather sparingly produced on the plants, were quite large and thick, much more so than in the ordinary no-botrytis type. In cultures numerous large, well-formed sclerotia appeared, some being an inch long and thick and solid (*fig. 41*, and *text fig. 1 a*). These sclerotia could be grown by the quart on suitable media, dishes of prune bread being especially favorable. Their development is similar to that of the smaller ones in the last type described. Beginning as a white, harder spot in the mycelium they gradually enlarge, becoming, when mature, black and hard. They have no connection with the substratum, being imbedded in the mycelium and easily separated from it. During their formation drops of a clear liquid usually appear on the surface, and in old cultures the sclerotia and mycelium often become incrusted with rod-shaped crystals of calcium oxalate. In cultures and on diseased plants organs of attachment are very abundant and entirely similar to those already mentioned.

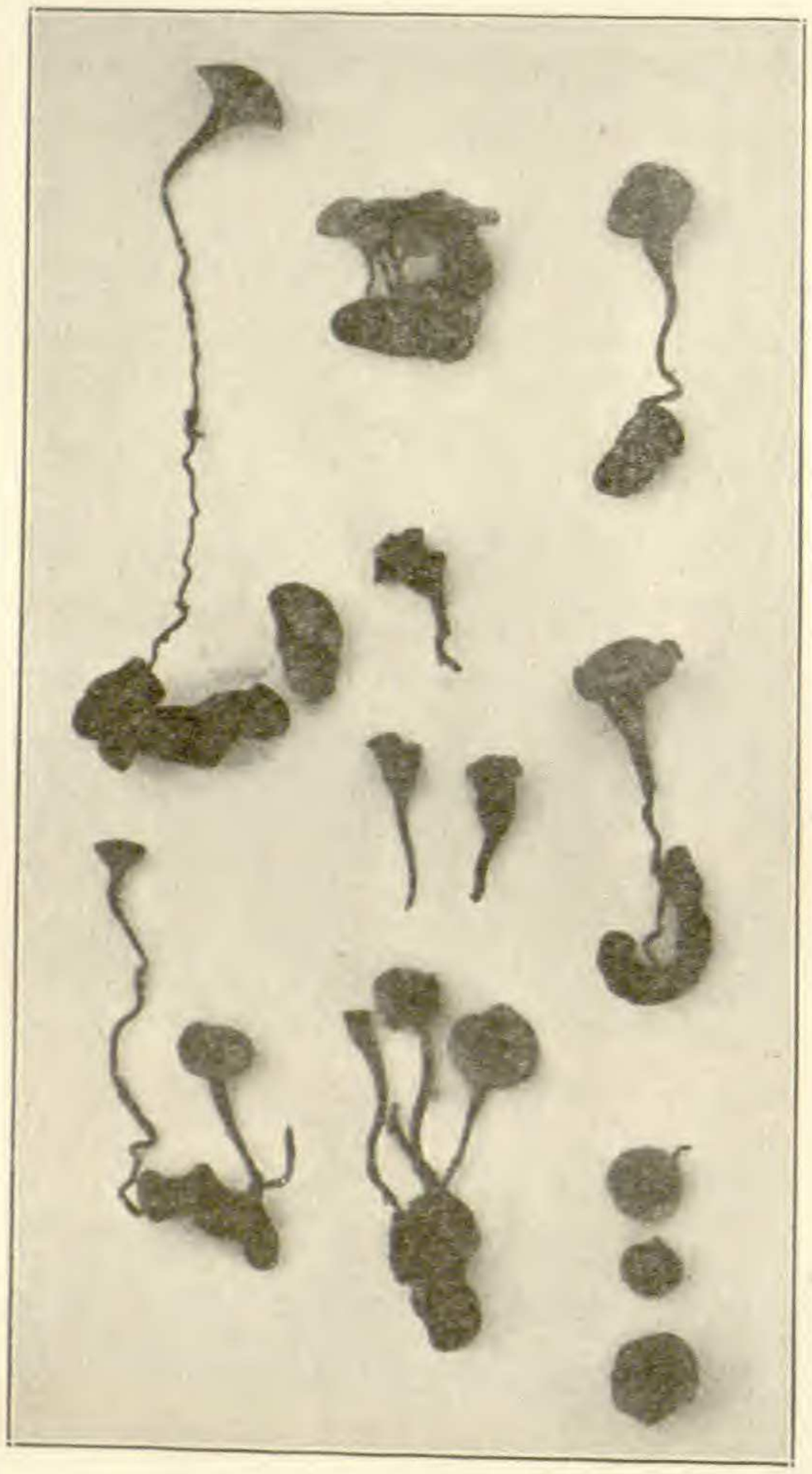

FIG. 2.—Sclerotia and apothecia of *Sclerotinia Libertiana;* slightly reduced.

When placed on wet sand these sclerotia soon began to throw up slender stalks, usually several from each, which expand into trumpet-shaped Peziza apothecia. These bodies varied somewhat in size and shape, as shown by the typical forms in *text fig. 2.*

The disks have the usual discomycetous structure as shown in section (*fig. 32*). Asci and paraphyses are shown more enlarged in *fig. 33*. This fungus was a typical form of *Sclerotinia Libertiana* Fckl. (*Peziza Sclerotiorum* Lib., etc.)

Similar infection experiments to those in the last case made with this material gave the same results. Diseased tissue or portions of mycelium never failed to produce the disease in healthy plants. No experiments have been made with ascospores in respect to infection. The conclusion is a safe one that *Sclerotinia Libertiana* is an active parasite of lettuce and, in some cases at least, the cause of the disease under consideration. The form just described, however, is far from common in greenhouses, and certainly does not occur in the great majority of cases of the "drop".

GENERAL CONSIDERATION OF THE CAUSE OF THE DISEASE.

These three types cover all the cases of the disease which have been seen by the writer. The last occurred in but a single lot of plants. The second represents the bulk of the disease in this state. The first in its purest form was found only in the single lot of plants described and occasionally in a few plants in a crop soon after setting. Cases are not rare, however, which appear to be a mixture of the first and second. Botrytis develops on affected plants but cultures from the most newly affected inner tissue give no Botrytis but characteristic growth of the no-botrytis form.

The observations thus far recorded are sufficient to establish the following statements:

The "drop," in the majority of cases, is a strictly parasitic disease and attacks the most vigorous plants.

The ordinary Botrytis in its conidial form does not cause the disease except in exceptional instances.

Either of the last two forms described is able to cause the disease in a strictly parasitic manner.

The disease is spread and infection takes place most commonly by saprophytic growth through the soil.

The fungus which causes most cases of the disease is able to exist indefinitely in the soil by means of sclerotia, which may be formed either upon affected plants or by purely saprophytic growth in the soil and appear to form the usual, if not the only, mode of reproduction.

This fungus may be exterminated by heating the soil.

In exceptional cases the "drop" appears to have been caused by the conidial form of *Botrytis vulgaris*, but only in plants which were under unfavorable conditions.

The disease may be caused by a typical form of *Sclerotinia Libertiana* Fckl., but this is exceptional.

In all cases of the disease there is the closest resemblance in the effect on the plant and in the parasitic mycelium which attacks it, the latter applying to the filaments and the organs of attachment which they bear.

The most marked differences between the three forms are found in the production of Botrytis conidia in the first and its absence in the other two; in the production of the Peziza stage in the last; in the form and size of the sclerotia and the manner of their production; and in the general greater development of the mycelium and its spread over the soil in the last two types.

On the basis of these statements the following suppositions are possible as to the relations of these forms to one another and the real cause or causes of the disease.

1. The three types are caused by three distinct species of fungi which are peculiarly coincident in certain respects.

2. The three types are caused by three different forms of the same species, which accounts for the coincidences.

3. Two of the forms belong to the same species while the third is distinct but similar in certain respects.

CULTURES.

In order to test further these hypotheses a large number of special cultures were made which may now be described. The specific object of these experiments was to find out, by growing the three forms of fungi under various conditions, whether any

of the forms could be changed into any other, or to prove definitely that they are all distinct. To accomplish the former required that Botrytis be developed in a pure culture of one or both of the no-botrytis forms, that one or both of the typical no-botrytis forms be developed from Botrytis conidia, or that the typical *Sclerotinia Libertiana* be developed from the ordinary no-botrytis form or *vice versa*.

Growth on various media.—Cultures of the three forms were made on a considerable variety of substances to test their effect on the organisms. These substances included various fruit decoctions, bread soaked with various nutrient juices and decoctions, and boiled fruits and vegetables of many different kinds. A detailed account of these cultures is unnecessary as in every case the growth was typical of the original material and no marked changes appeared.

Effect of low temperature.—Here again no results were obtained. It was found that each of the forms, with proper nourishment, continued to grow almost down to the freezing point, but naturally with much less vigor at the lower temperatures. No other effect than this was observable with the no-botrytis forms. With Botrytis no conidia developed in cultures kept below 5° C., a feeble mycelium being the only growth. When put in a warm place, however, these cultures at once grew in the ordinary manner, producing abundant conidia.

Effect of darkness.—No marked effect was produced by growth in total darkness.

Effect of starvation.—Cultures made in pure gelatine with no nutrient addition showed nothing more marked than a feeble growth.

Effect of solidity of substratum.—This was tested by using nutrient agar of different degrees of solidity. Growth was not as vigorous upon the hardest grades, but no other effect appeared.

Effect of acid and alkaline media.—These experiments were made by using as a nutrient medium prune juice of different degrees of acidity and alkalinity. The decoction was first carefully neutralized by an experienced chemist, using sodium

hydrate and tartaric acid weighed out in the dry form and added to the prune juice in the proper amounts; the following series of flasks were made up: $\frac{1}{10}$, $\frac{1}{2}$, 1, 2, 3, 4, 5, and 10 per cent. acid, with similar alkaline series.

With Botrytis no results affecting the main question were obtained from these cultures. After four days good mycelium and conidia had developed in alk. $\frac{1}{10}$ per cent., neutral, and $\frac{1}{10}$, $\frac{1}{2}$, and 1 per cent. acid. Acid 2 per cent. had considerable mycelium, rather dense, and a few conidiophores. Acid 3, 4, and 5 per cent. had a smaller amount of dense mycelium, forming a compact membrane. Acid 10 per cent. had merest trace of development. Alk. $\frac{1}{2}$ per cent. had good mycelium, loose and flocculent, with some conidiophores around the edges. Alk. 1 per cent. about the same but with very few conidiophores. Alk. 2 per cent. poorer mycelium with woolly, flocculent appearance and no conidia. Alk. 3 per cent. merest trace of development. Alk. 4, 5, and 10 per cent. no growth. Two weeks later conidia were abundant in all the acids except the 10 per cent., which showed no growth. The alkalies had quite abundant conidia below 3 per cent., but from there on very little or no development. Acid 1 per cent. gave about as vigorous and typical a Botrytis growth as any. The contrast was very marked between acid 2–5 per cent. and alk. 1–2 per cent. The former formed a close dense membrane, while the latter was loose, woolly, and flocculent. No particular difference in the filaments could be seen with the microscope. While these results have some little general interest they gave no evidence as to a connection between Botrytis and other "drop" fungi. The no-botrytis fungus with small sclerotia showed no such striking differences in development in acid and alkaline media as did Botrytis. Its range of growth was about the same and the effect upon the mycelium was somewhat similar but by no means as marked. From one culture of this sort, however, a valuable result was obtained. This was a large flask of prune of considerable alkalinity but not made up in definite proportions. It was inoculated with mycelium from a pure culture of the small-sclerotia fungus, coming

originally from lettuce in a house which had never contained any other form of the disease. In this culture the usual small sclerotia were first produced, but later there appeared a considerable number of larger ones, appearing similar to those of *S. Libertiana*. A number of these were obtained and cultures made from them on ordinary prune bread, with the result that the typical large-sclerotia type developed. No spores of this type had ever been developed in the laboratory at the time this culture was made nor had any trace of the large-sclerotia form ever appeared in connection with any of the material used, so that there would seem to have been no possible chance for accidental infection. Consequently the only possible explanation seems to be that *Sclerotinia Libertiana developed directly from the small-sclerotia, no-botrytis form.*[3] (In this connection should be borne in mind the fact already mentioned that in one case one of the small sclerotia started to develop an apothecium just as in *S. Libertiana*.)

CONCLUSIONS.

From all the observations and experiments thus far recorded it is concluded:

1. That the lettuce "drop" in Massachusetts is caused by two distinct species of fungi, namely, *Botrytis vulgaris* Fr. and *Sclerotinia Libertiana* Fckl., which are remarkably alike in some respects and have an entirely similar effect upon the plant.

2. That the bulk of the disease is caused by a degenerate form of the latter species, which has almost entirely lost the ability to reproduce by spores but which is highly specialized as a vegetative, facultative parasite.

3. That the disease is caused by *Botrytis vulgaris* and the typical *Sclerotinia Libertiana* in mature plants only in rare instances; the former on account of its inability to attack vigorous plants under normal conditions, the latter because of its infrequent occurrence.

[3] It is not asserted that this result is to be attributed to the alkalinity of the culture medium.

4. That in many cases Botrytis develops as a saprophyte on plants primarily affected by the other species and is mistaken for the true parasite on account of the similarity of the mycelium.

5. That these forms and species can be distinctly separated by means of pure cultures, and distinguished from one another by the form and manner of growth of the sclerotia.

NOTE.—No reference has thus far been made to the internal structure of the sclerotia. De Bary (Morph. and Physiol. p. 31) draws a distinction between the Botrytis and *Scl. Libertiana* forms on the basis of structure, but the writer has not been able to establish this or make a uniform distinction. *Fig. 39* shows a section which might represent any of the forms.

Thus it appears from the study of this disease that *Sclerotinia Libertiana* has no connection with the Botrytis form in question, although at first sight this appeared to be undoubtedly the case. Confusion has arisen from the similarity in the parasitic mycelium of the two forms, their similar effect on the plant and their frequent simultaneous occurrence; coincidences most deceptive to superficial examination but easily explained on the ground of the close relationship between the two species. Too general conclusions should not be drawn from the case of this disease, however, without taking into consideration a number of very similar ones which have been described. The writer has been fortunate in obtaining material of a number of these diseases, as well as additional information concerning some of them, and has spent considerable time in comparing them with the results obtained from the study of the lettuce disease. Careful inquiry shows at once that much has been taken for granted in many of these cases and conclusions drawn which were based more on apparent probability and general appearances than actual proof. It must be conceded that in a number of cases which are mentioned hereafter the conclusion seems at first sight fully warranted that *Botrytis cinerea* is a stage in the life history of *Sclerotinia Libertiana*, so intimately are the two forms associated with one another and so similar are they in effect and many details of structure. But, as will presently appear, in every case which the

writer has been able to investigate or obtain full information about, as well as from his general study of the species of fungi concerned, the conclusions based on the study of the lettuce disease are fully substantiated. Three classes may be made of the diseases of this nature as follows: (1) diseases where both *Sclerotinia Libertiana* and *Botrytis cinerea* (*vulgaris*, etc.) appeared; (2) diseases attributed to Botrytis alone; and (3) diseases attributed to Sclerotinia alone.

II. Diseases attributed to Sclerotinia and Botrytis.

As a type of this class, which would include the lettuce disease, may be taken the disease of hemp described by Behrens and others.

HEMP DISEASE.

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1. TICHOMIROFF, W. *Peziza Kaufmanniana;* eine neue, aus Sclerotium stammende und auf Hanf schmarotzende Becherpilz-Spezies. Bull. Soc. Nat. de Moscou.— : 294. 1868.

2. HAZSLINSZKY, F. *Polyactis infestans.* Grev. 6 : 77. 1877.

3. DE BARY, A. Ueber einige Sclerotinien und Sclerotinienkrankheiten. Bot. Ztg. 44 : 378. 1886.

4. BEHRENS, J. Ueber das Auftreten des Hanfkrebses in Elsass. Zeitschr. f. Pflanzenkrankh. 1 : 208. 1891.

5. SORAUER, P. (*a*) Die Schäden der einheimischen Kulturpflanzen. (Zeitschr. f. Pflanzenkrankh. 1 : 212. 1891.)
(*b*) Hanfkrebs. Pflanzenkrankheiten 289.

6. HILTNER, L. Einige durch *Botrytis cinerea* erzeugte Krankheiten. Inaug. Diss. 1892.

7. FRANK, A. B. Sclerotienkrankheit des Hanfes. Die Pilzparasitären Krankheiten der Pflanzen 499.

A disease very similar to that of the lettuce is described by Behrens (4) on hemp. For several successive seasons a stem rot of this plant was observed in Alsace. Affected stems were permeated with large, intercellular filaments, while upon the surface appeared sclerotia resembling the old form *Sclerotium varium*. In the interior cavity of the stem were also numerous sclerotia. Upon some affected plants a growth of *Botrytis cinerea* appeared,

the mycelium of which agreed entirely with that in the stem. In a moist chamber Botrytis appeared on many of the plants. Material received the following year showed no trace of Botrytis; otherwise the disease was exactly the same. Cultivated on bread the fungus produced abundant sclerotia but no Botrytis, while in the previous year the conidial form appeared in cultures regularly. The author concludes that the organism is similar to *Sclerotinia Libertiana* in every way except for the Botrytis conidia, which form is supposed to characterize *S. Fuckeliana*, and states that one of two cases is possible; either the Botrytis is secondary on stems affected primarily with *S. Libertiana*, or else the fungus occurs varyingly, with or without Botrytis conidia. The results of inoculation experiments with Botrytis conidia appeared to support the latter hypothesis, that the Sclerotinia may appear with or without Botrytis. Whether it should be called Fuckeliana or Libertiana the author was unable to decide.

Some time after the above was published, in the spring of 1898, the writer visited Dr. Behrens at Karlsruhe and was informed by him in regard to this disease that after more extended observation and consideration he inclined to the opinion the Botrytis and Sclerotinia might after all have been distinct species on the hemp, having no connection with one another.

Tichomiroff (1) found a disease of hemp in Russia with which that described by Behrens appears to be identical. He observed numerous sclerotia and named the form *Peziza Kaufmanniana*. No mention is made of a Botrytis stage. De Bary (3) found it possible to infect hemp with ascospores of *Sclerotinia Libertiana* and decided that *Kaufmanniana* was the same species.

Hazslinszky (2) found a fungus parasitic on hemp in Hungary which he named *Polyactis* (*Botrytis*) *infestans*. Behrens considered this as probably a form of *B. cinerea*, although the conidiophores, as figured by Hazslinszky, are articulated in a peculiar manner.

Hiltner (6) found a hemp disease with symptoms agreeing with those described by Behrens, Tichomiroff, and Hazslinszky, wherein no sclerotia appeared but abundant *Botrytis cinerea*.

The writer was unable to obtain material of this disease and consequently has no original information to offer concerning it. This case has been brought forward as one of the best examples of the connection between Botrytis and *Scl. Libertiana*, but Dr. Behrens' later statement changes the aspect completely. With his original conclusions discredited by himself there remains the fact that Tichomiroff and Hiltner found the disease caused respectively by Sclerotinia and Botrytis alone, and no proof is to be found that the two forms had any connection with one another in attacking this plant. The fact that Behrens found no Botrytis in connection with the disease during one season gives further evidence that this species was entirely distinct, though in similar effect and appearance.

RAPE DISEASE.

BIBLIOGRAPHY.

1. HAMBURG, E. A. *Peziza ciborioides* Fr., etc. III. Földniv. Erdec. 8:509. 1880. (Bot. Centralb. 8 : 172. 1881.)
2. DE BARY, A. *loc. cit.* 458.
3. FRANK, A. B. Sclerotienkrankheit des Rapses. *loc. cit.* 493.
4. SORAUER, P. Die Sclerotienkrankheit des Rapses. *loc. cit.* 297

The disease of the rape plant described by Frank (3) is also one of interest in this connection. Plants were found to be affected by a rotting of the stem, the cortex and pith being filled with a fungous mycelium, soon becoming completely destroyed. Numerous black sclerotia were present in the pith cavity. The filaments of the mycelium were hyaline, filled with granular protoplasm with vacuoles, septate and branching profusely in all directions. The largest had a diameter of 20μ. The sclerotia were of irregular form and had a diameter of 2–10^{mm}. In places where the plants stood close together *Botrytis cinerea* often appeared upon the diseased portion of the stem. When affected stems were put under conditions of moisture this always occurred. The Botrytis hyphae seemed to arise without doubt from the interior filaments. Further development was obtained by placing sclerotia on moist sand, when they produced

apothecia, which the author attributes to *Sclerotinia Libertiana*. It was found possible to infect healthy rape plants with either conidia, ascospores, or mycelium, or by sowing the seed in a pot of earth containing diseased tissue. Seedlings were infected with Botrytis conidia and kept under a bell jar. They soon showed the disease as before. The author also cites the results obtained by Hamburg (1), who found it possible to infect healthy rape plants with ascospores of *S. Libertiana*, producing the disease with a development of Botrytis conidia, and he (Frank) concludes that the distinction of the two species *S. Libertiana* and *Fuckeliana* on the basis of presence or absence of the Botrytis form is impossible.

De Bary (2) discredits Frank's conclusions as to the connection between *S. Libertiana* and Botrytis.

This case seems to be the strongest argument in support of the connection between Botrytis and *Scl. Libertiana*. The writer has no personal knowledge of the disease. It should be pointed out, however, that Frank's results are really but little different from those obtained in the study of the lettuce disease where opposite conclusions were reached. The principal evidence in favor of the connection between the two forms is based on their simultaneous occurrence and the fact that the disease was induced in healthy seedlings kept under a bell jar by infection with Botrytis conidia, both of which facts apply equally well to the lettuce disease as already described. Nor are Hamburg's results any more convincing, since the appearance of Botrytis as a saprophyte on plants attacked by Sclerotinia is no unusual occurrence. The appearance of Sclerotinia (meaning sclerotia capable of producing Peziza) upon plants infected with Botrytis conidia would have carried great weight, but no such result has been obtained. The writer feels justified in stating in regard to this disease, on the testimony of those who have described it, and in the light of the similar cases which he has investigated and the general study of the species concerned, that no positive proof whatever is found herein that *Botrytis cinerea* and *Sclerotinia Libertiana* have any connection with each other.

POTATO DISEASE.

BIBLIOGRAPHY.

1. SMITH, W. G. (*a*) New form of disease in potatoes. Gard. Chron. N. S. **14** : 264. 1880.

(*b*) Disease of potatoes. Nature **28** : 299. 1883.

(*c*) New disease of potatoes. Diseases of field and garden crops 15.

2. Nature **28** : 231. 1883.

3. WILSON, A. S. (*a*) Disease of potatoes. Nature **28** : 343. 1883.

(*b*) Potato disease. Gard. Chron. N. S. **20** : 333. 1883.

4. BLYTT, A. Disease of potatoes. Nature **28** : 367. 1883.

5. DE BARY, A. *Loc. cit.* 436.

6. COHN, F. Illustr. landw. Ztg. 1887.

7. KIRCHNER, O. Die Stengelfäule, eine neue auftretende Krankheit der Kartoffeln. Würmtembergisches Wochenblatt für Landwirtschaft **30** : —. 1893.

8. RITZEMA BOS, J. (*a*) Kurze Mittheilungen über Pflanzenkrankheiten und Beschädigungen in den Niederlanden in den Jahren 1892 und 1893. Zeitschr. f. Pflanzenkrankh. **4** : 144. 1894.

(*b*) Kurze Mittheilungen, etc., im Jahr 1894. Zeitschr. f. Pflanzenkrankh. **5** : 286. 1895.

9. SORAUER, P., Editor. Einige Notizen über die in den letzten Jahren in Deutschland aufgetretenen Krankheitserscheinungen. Zeitschr. f. Pflanzenkrankh. **5** : 97. 1895.

10. REHM, H. Ascomyceten. Rabenhorst's Kryptogamen Flora **13** : 803.

11. FRANK, A. B. Sclerotienkrankheit der Kartoffel. *Loc. cit.* 500.

Kirchner (**7**) found potato plants which showed symptoms very similar to those in the lettuce, the stem rotting off just above the ground. Where the plants stood close together a vigorous growth of *Botrytis cinerea* appeared upon the affected parts, to which the author attributes the disease. No sclerotia were found. Ritzema Bos (**8**) found the same disease abundant in Holland. Cohn (**6**) notes a potato disease in Germany with very similar symptoms, but found sclerotia which seemed to belong to *Sclerotinia Libertiana*. The same is stated as being abundant in Norway. A "new disease of the potato" has been described by Smith (**1**), Wilson (**3**), and Blytt (**4**). The diseased plants became covered with a thick, felt-like growth of fungous mycelium, and in a short time stem and leaves were completely destroyed. Immersed in the mass of mycelium

appeared numerous black sclerotia, ranging in size from that of a grain of sand up to a small bean. From such sclerotia a Peziza form was obtained, which is shown, copied from Smith's figure, in *fig. 37*. The form was described by Berkeley and Wilson (3b) as a new species, under the name *Peziza postuma*. De Bary (5), however, to whom the material was sent, determined the fungus as *Sclerotinia Libertiana*. *Peziza postuma* is also given by Rehm (10, p. 816) as a synonym of *S. Libertiana*. In each of these cases the disease appears to have been caused by Botrytis or Sclerotinia alone, and no reason appears for claiming a connection between them.

CUCUMBER DISEASE.

BIBLIOGRAPHY.

1. HUMPHREY, J. E. Diseases of the cucumber plant. A sclerotium disease. Rept. Mass. Exp. Sta. 10 : 212. 1893.

2. COOKE, M. C. Cucumber diseases. Gard. Chron. III. 14 : 137. 1893.

The disease described by Humphrey (1) under the name of "timber rot" is not uncommon in cucumber houses in Massachusetts. The writer has met with it several times and also has received specimens from the New York Exp. Sta. at Geneva. Cooke (2) notes the occurrence of apparently the same trouble in England. The disease is characterized by a dry rot of the stem with a production of mycelium and sclerotia upon the surface. From the sclerotia *Sclerotinia Libertiana* readily develops. The writer has found no conidial form in connection with the disease. Humphrey, however, finding Botrytis on a decaying fruit, argues a connection between the forms. He obtained sclerotia in cultures from conidia which are stated to have shown complete identity in microscopic structure with sclerotia developed from the ascospores of the Sclerotinia. The form and manner of growth of the sclerotia were not the same, but this difference was ascribed to the nature of the substratum.

Humphrey's results have been repeatedly duplicated by the writer. It is true that Botrytis is often found on rotten cucumbers, and also that in cultures from conidia sclerotia may be

obtained indistinguishable in microscopic structure from those of *Sclerotinia Libertiana*. This has already been shown in connection with the lettuce disease. It was also shown there, however, that the form and manner of production of the sclerotia is highly characteristic and not affected by the substratum. There is, in short, no reason whatever for supposing, from this case, any connection between Botrytis and Sclerotinia except their occurrence in the same house. The entire distinctiveness of the two forms is nowhere more easily demonstrated than in such a case as this.

VEGETABLE, BULB, AND FRUIT ROTS.

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5. KISSLING, E. Zur Biologie der *Botrytis cinerea*. Hedw. 28:227. 1889.
6. HALSTED, B. D. Fungous diseases of various crops. Rept. N. J. Agrl. Coll. Exp. Sta. 3:350. 1891.
7. MASSEE, G. (*a*) An onion disease. Gard. Chron. III. 16:160. 1894.
(*b*) Onion Sclerotinia. Text-book of plant diseases 156.
8. POTTER, M. C. Rottenness of turnips and swedes in store. Journ. Board of Agr. 3:120. 1896.)
9. WEHMER, C. Untersuchungen über die Fäulniss der Früchte. (Zeitschr. f. Pflanzenkrankh. 6:173. 1896.)
10. OUDEMANS. Ned. Kruidk. Arch. II. 4:260.
11. SORAUER, P. Pflanzenkrankheiten.
12. FRANK, A. B. Die Pilzparasitären. Krankheiten der Pflanzen.

One of the most common cases of trouble caused by Botrytis and Sclerotinia is the rotting of various fruits, vegetables, etc. The writer has investigated a case of rotting of turnips found in Munich, Germany. Affected roots were not foul or badly decayed except in the worst affected portions, but showed

simply a slight discoloration and moist appearance of the flesh, no outward change appearing. No fungus was visible at first to the naked eye. When cut in two and kept moist over night a vigorous growth of *Botrytis cinerea* appeared on the affected parts, most abundant where worst affected and shading off toward the most recently affected portion, where no conidia developed. The interior was found to be filled with a vigorous mycelium similar to that in the lettuce and other diseases (*fig. 49*). Cultures on various media gave the usual Botrytis development, conidia being developed abundantly when badly affected tissue was used for infection, but very sparsely on newly affected portions or in cultures made therefrom. In the latter cultures sclerotia were quite numerous, being long, narrow, and thin, closely joined to the substratum in the characteristic Botrytis manner. It was found possible to infect sound roots with conidia by cutting out a plug, inserting the spores, and replacing the part cut out. There was no question that the rotting in this case was caused by *Botrytis cinerea*, pure and simple. The case described by Potter (8) is entirely similar. De Bary (4) and Coemans (1) found rotting of turnips, carrots, etc., caused by *Sclerotinia Libertiana* (*Peziza Sclerotiorum*). The writer has found by infecting turnips with Botrytis and Sclerotinia that an entirely similar effect is obtained and an intercellular mycelium produced which is quite indistinguishable. By making cultures, however, from the affected tissue, sclerotia are obtained, and in the one case conidia, which distinguish the two forms at once. This case, therefore, shows once more how easily confused these two forms are, having so similar a mycelium and effect, while at the same time it furnishes strong proof, when thoroughly looked into, of their entire distinctness.

Rotting of various fruits caused by Botrytis has been described by Brefeld (2) and Wehmer (9).

A rotting of onions is often caused by Botrytis and has been described by Halsted (6), Sorauer (11, p. 294), and Frank (12, p. 503). The writer found a similar case in Munich, where the affected tissue was permeated with a mycelium (*fig. 48*).

The Botrytis in this case was not a typical *cinerea*, having a low, dense manner of growth which persisted in cultures for many generations. The conidiophores were also short and stout (*figs. 5, 6*), and the conidia small and rather pointed as in **12**, plate 1. No sclerotia were found. Massee (**7**) ascribes the onion rot to *Sclerotinia bulborum* Wak. and figures (**7a**) a Botrytis apparently identical with *B. cinerea*, and a Peziza form showing no apparent distinction from *Sclerotinia Libertiana*. *Sclerotinia* (*Peziza*) *bulborum* was described by Wakker (**3**) as the cause of a hyacinth disease, a very interesting case in connection with the lettuce disease on account of its very similar mode of spreading and existence in the soil. No Botrytis stage was found, and Oudemans (**10**) states that none occurs. *Fig. 38* is copied from the latter. From all appearances it is doubtful whether the form described by Massee is the same as that of Wakker, and certainly the connection of the Botrytis and Sclerotinia forms, and their distinctness from the ordinary species, need further demonstration. An endless amount of confusion of these forms already exists on account of the multiplication of species for every new host.

III. Diseases caused by Botrytis alone.

No fungus is more common on dead or dying plant tissue than the common form of Botrytis. Not only is it abundant as a saprophyte, but cases often occur where it is a true parasite. Accounts of such cases are innumerable in botanical literature, but only a few can be briefly cited here. The species of Botrytis concerned has many different names, as has already appeared. In general it may be said that in Europe the ordinary form is referred to *B. cinerea* Pers., while in America the equally abundant species is usually called *B. vulgaris* Fr. These forms have been often regarded as identical, and the writer is able to state definitely that such is the case. Material from various parts of America and Europe has been carefully compared, both by examination and in cultures, from which it has been clearly shown that the forms are completely identical. On the basis of priority *cinerea* should be the specific name adopted, though, as

Wehmer[4] points out, *vulgaris* is more appropriate for so universal a species.

The following disease is a good type of this class:

A NEW DISEASE OF THE LINDEN.

In the spring of 1898, while working in Professor R. Hartig's laboratory at the University of Munich, the writer received several specimens of *Tilia parvifolia* which had been found in the nursery by Dr. von Tubeuf and appeared to be diseased. They were found among a considerable number of small saplings three to five feet high, growing close together in the usual nursery beds. At this time most of the trees were entirely leaved out, but these individuals had been noticed on account of their buds being not yet unfolded, though still green and apparently sound. The branches and upper part of the stem were also green and fresh, showing no abnormal symptoms, and the same was true of the roots. But in the lower part of the stem, from the surface of the ground up to a height of several inches, an abnormal condition was evident. Upon the surface of this part of the stem numerous excrescences were found, breaking out through the epidermis, with a thickness of about 0.5^{mm}, and varying greatly in shape and size. Some were nearly round, others irregular, and still others long and narrow, extending parallel with the stem, or more often around it. The latter form had a maximum length of about 2^{cm}, while the more circular ones had a diameter of 0.5^{cm}, or less. They had a dusty gray color and gave the stem an appearance somewhat like that of one affected with a Peridermium. *Text fig. 3* is from an excellent photograph of an affected stem, made by Dr. von Tubeuf. It was evident that the production of these excrescenses was proceeding from below upward, as the longest were just above the surface of the earth, while further up on the stem very small ones were just breaking out through the epidermis. In the affected part of the stem the wood and bark were discolored and evidently dead, but above and below it the tissue

[4] Zeitschr. f. Pflanzenkrankh. 4: 209. 1894.

was still fresh and sound. The bark appeared to be first affected, as it was always discolored somewhat in advance of the wood. Upon examining the outward excrescences it was found that the dusty appearance of the surface was due to a dense growth of a form of Botrytis, much like *cinerea*, but not entirely agreeing with the typical form. The conidiophores were very stout and thick, averaging 20μ in diameter, and the conidia large and very various in shape, many being nearly 30μ in length (*fig. 10*). In cultures the form at once reverted to the typical *cinerea*, showing that it belonged to that species. Further examination showed that these excrescences were a sort of half-formed sclerotia, having the usual cellular structure at the base, but lacking a definite surface layer and resolving above into a dense mass of conidiophores. *Fig. 40* shows a section of one of these sclerotia. They originate in the cortical parenchyma, being separated by the bast layer from the wood. Besides these sclerotia the cortical parenchyma was found to be permeated by a vigorous mycelium about as in the other diseases described. The affected tissue was being rapidly destroyed, but the bast layer seemed to be little affected and no filaments could be found in the wood except a few in the most outer portion.

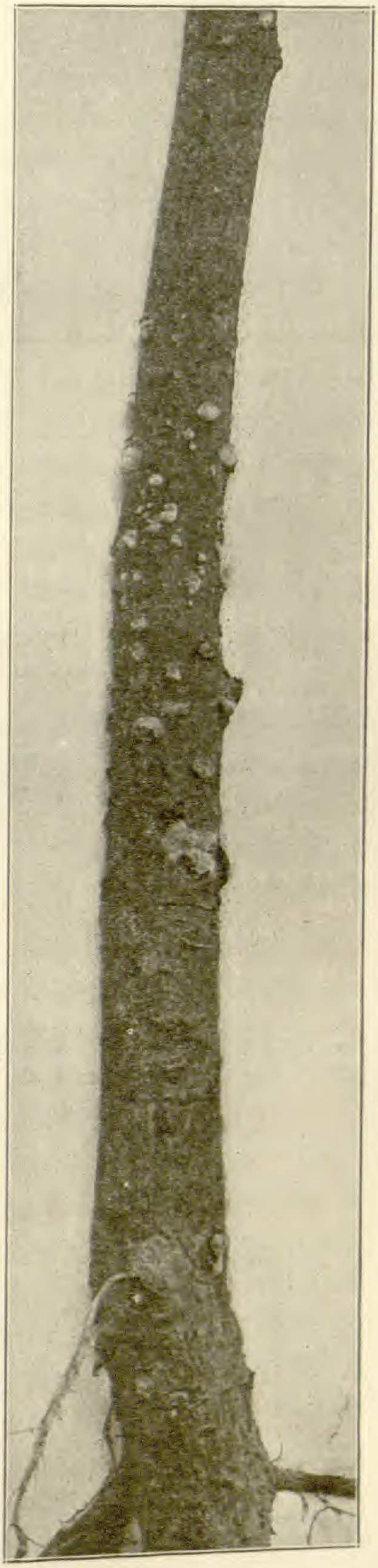

FIG. 3.—Linden stem attacked by Botrytis.

The affected portion of a stem was split in two and the two halves placed in a moist chamber. In one night a luxuriant Botrytis growth developed, being confined entirely to the cortex, most abundant in the worst affected portion and shading off gradually in the direction of what had been the upper part of the stem. Toward the boundary between the affected and unaffected areas no Botrytis appeared, but an abundant mycelium. In this portion, *i. e.*, the most newly affected, there appeared later ordinary black sclerotia having a long narrow form and located in the cortex, especially along the cut edges. The Botrytis gradually advanced, but was much more abundant back in the older part. Gelatine cultures were made with conidia and portions of the affected bark. The former produced a considerable mycelium, rather few conidia, and some sclerotia. The latter developed a similar mycelium,very few conidia, and numerous, larger, roundish sclerotia. Cultures were also made in the portions of the vegetative mycelium which appeared in the moist chamber upon the most newly affected portion of the stem (where no Botrytis appeared). This gave a vigorous mycelium with sclerotia, but no Botrytis. All of the sclerotia obtained from this material showed the characteristics of those of the botrytis type of the lettuce disease, being thin and joined with the substratum.

Several more affected trees were found in the nursery, both *Tilia parvifolia* and *T. grandifolia*. These showed the same symptoms as before. Some that were most affected seemed to be quite dead, and in the lower part of the stem the bark was quite destroyed, the wood being laid bare, but covered more or less with shreds of the bast which still remained. A few ordinary black sclerotia were found, but most were of the half-formed variety, covered with Botrytis. These appeared to have developed the previous fall, producing conidia in the spring.

The main features of this disease are these: a vigorous mycelium, starting apparently at the surface of the ground, proceeded upward through the cortical parenchyma, completely destroying it and eventually killing the plant. Sclerotia were developed upon the surface but reverted to the production of

conidia of *Botrytis cinerea* before becoming mature. This may have been due to the coming on of winter before the sclerotia were fully formed; at any rate the fungus was able to develop sclerotia and conidia in the usual manner, as shown in cultures and the moist chamber. It is believed that this disease was caused solely and primarily by *Botrytis cinerea*, in this case a true parasite. Cultures and observations showed throughout the same characteristics as found in Botrytis in connection with the lettuce disease and there is no reason to suppose that any other species was involved. This interesting disease upon the linden appears to be an entirely new one, and is the first of this class to be reported upon a woody plant. Its similarity, however, to some of the other stem rots herein described is apparent.

BOTRYTIS ON ROSE TWIGS.

Some twigs of hothouse roses were obtained in Munich by the writer, which were affected by a dying away of the tips, the disease gradually extending down the stem. The extreme tips were entirely dead and covered with a Botrytis growth. Further down the stems were turning black and dying, but no Botrytis was visible. Sections showed that the interior of affected parts of the stem was full of filaments. In the worst affected parts the whole tissue was destroyed and Botrytis conidiophores were growing out through the surface. In the less affected parts it was found that the disease advanced by large filaments which grew at first through the area of bast fibers, entirely disorganizing this tissue before the rest was at all affected. Later the whole stem became included. *Figs. 46* and *47* show cross and horizontal sections of affected twigs with the filaments among the bast fibers. It appeared in this case, as in several others already described, that the most actively parasitic filaments which attack new tissue bear no conidia, the latter appearing later on the older parts. The species was the usual *cinerea* but was especially luxuriant, bearing large, many-branched conidiophores. No sclerotia were found upon the limited material at

hand, but cultures from the Botrytis gave at first conidia and later sclerotia of the usual botrytis type.

Among the many other diseases of this class which have been described, space only permits that the following be mentioned:

CONIFERS.

TUBEUF, K. F. von. Bot. Centralb. 33:347. 1888. Also: Beiträge zur Kenntniss der Baumkrankheiten. Pflanzenkrankheiten 283.
BEHRENS, J. Zeitschr. f. Pflanzenkrankh. 5:136. 1895.
RITZEMA BOS, J. Forstlich-naturwiss. Zeitschr. 6:174. 1897.
MASSEE, G. Text-book of plant diseases 160.

GRAPE.

MÜLLER–THURGAU, H. Landwirtsch. Jahrb. 17:83. 1888.
VIALA, P. Rev. gén. de bot. 3:145. 1891. (Zeitschr. f. Pflanzenkrankh. 7:159. 1897.)
RAVAZ, L. Compt. rend. 118:1289. 1894. (Zeitschr. f. Pflanzenkrankh. 5:49. 1895.)
CUBONI, G. Bull. di Notizie Agrarie. 2:487. 1896. (Zeitsch. f. Pflanzenkrankh. 7:159. 1897.)
VON BABO UND MACH. Weinbau.

LILY.

WARD, H. M. Ann. Bot. 2:319. 1888. Diseases of plants 117.
KEAN, A. J. Bot. Gaz. 15:8. 1890.
MASSEE, G. Text-book of plant diseases. 161.

HORSE CHESTNUT.

KISSLING, E. *Loc. cit.*

PRUNUS TRILOBA.

TUBEUF, K. F. VON. Pflanzenkrankheiten 281.

GENTIAN.

KISSLING, E. *Loc. cit.*
PRILLIEUX ET DELACROIX. Bull. Soc. Myc. de France 6:135. 1890.

CYCLAMEN AND PRIMULA.

WEHMER, C. *Loc. cit.*

In all these cases the general nature of the disease was the same, Botrytis appearing more or less on affected parts and often forming sclerotia. Many interesting points are brought out in some of the descriptions, but they have little bearing on the question under consideration. It may be mentioned that the

Botrytis Douglasii of Tubeuf is without any doubt a form of *B. cinerea*, as the writer has ascertained by examination of the original material in cooperation with Dr. von Tubeuf. In Professor Ward's lily disease the species was thought to be distinct from *cinerea* on account of the large size of the conidia (20–25 × 15μ). The writer has often found the ordinary species with spores as large as 30–15μ, however, and it would seem from Professor Ward's figures of the conidiophores that the form must be very close to *cinerea*. In some of these cases, notably that of the grape, the Botrytis is referred to *Sclerotinia Fuckeliana* De By., its supposed Peziza form, which is said to develop from sclerotia on affected grapes. This form is unknown to the writer, but has been held by De Bary to be the real mature form of *Botrytis cinerea*. Pirotta (N. Giorn. Bot. Ital. **13**: 130. 1881) has also described *Fuckeliana* as distinct from *Libertiana*, but it is apparent in almost all cases where *B. cinerea* is referred to as *Scl. Fuckeliana* that nothing more was observed than the ordinary conidial form and possibly sclerotia. Whether or not this is the true perfect form of *cinerea*, it is certain that the connection has never been proved directly, and much has been taken for granted by various writers upon no foundation whatever.

IV. Diseases caused by Sclerotinia Libertiana alone.

Cases are not rare of *Sclerotinia Libertiana* attacking plants when no Botrytis appeared. The cucumber disease already described is really one of this sort, as the Botrytis simply happened to occur in the same house. The writer has seen water cress and parsley in greenhouses attacked by this species, such cases being not uncommon in the Boston houses where these plants are considerably grown. Tomatoes also occasionally show the same trouble, rotting at the surface of the ground. The Peziza form is occasionally found developing from sclerotia in the soil in such houses.

De Bary (*loc. cit.*) describes a stem rot of Zinnia, Petunia, and other plants caused by this species. It is also not uncommon upon Helianthus. Dr. O. Kirchner, of Hohenheim, gave

the writer Peziza-bearing sclerotia from such a disease of this plant. Pammel (Trans. St. Louis Acad. **6**: 191. 1893) has described a similar disease. W. G. Smith (Gard. Chron. III. **8**: 324. 1890 and III. **9**: 791 1891) describes a stem rot of hollyhocks caused by *Scl. Libertiana*. The disease was entirely similar in all these cases and needs no extended description. The stem of affected plants rotted just above the ground, being filled with a vigorous mycelium as in the diseases already described. Sclerotia were produced both upon the surface and in the interior cavity of the stem, from which the Peziza form readily developed.

A disease of clover has been described by several writers which is very similar to those under consideration but ascribed to *Sclerotinia Trifoliorum* Erik. which is regarded as distinct from *Libertiana* though apparently very similar. The writer received alfalfa plants from Mr. F. C. Stewart of the New York Exp. Station which were supposed to be affected with this species. The sclerotia, however (*text fig. 1 e*), both from diseased stems and cultures, were entirely similar to those of *Libertiana*, and produced a Peziza form which left no doubt that it was that species.

V. General conclusions on Sclerotinia Libertiana and Botrytis cinerea.

During the four years in which this work has been carried on a great deal has been done which has no special connection with that part of the subject with which the present article deals. A large amount of material has been obtained and the fungi grown and studied under all sorts of conditions. Most of the results which it is intended to emphasize here have already been brought out in various places in this description. It is maintained above all *that Sclerotinia Libertiana and Botrytis cinerea have no connection whatsoever with each other, and that the former species has no conidial stage of this type*. Growing either as a saprophyte or parasite, it shows at all times a mycelium composed of large, branching, septate filaments, averaging about 10–15 μ in diameter, which produce

organs of attachment abundantly when in contact with any hard substance. Sclerotia are always produced abundantly in cultures and upon affected plants. These vary in size up to an inch in length, having an irregular form, but are solid and "meaty" and produced embedded in the mycelium, having no connection whatever with the substratum. The Peziza form is readily obtained from them. The internal structure of these sclerotia consists of a mass of thickened filaments knotted closely together and surrounded by a black, cellular layer. This species is a typical example of a facultative parasite, being able to exist indefinitely as a saprophyte but at the same time capable of attacking a great variety of plants in a strictly parasitic manner.

Botrytis cinerea is without doubt a closely related species, and has many points of resemblance. It is not as strongly parasitic as the other species, attacking living plants more commonly only when they are under unfavorable conditions or when injured in some way. At times, however, it appears to be a true parasite. When growing as a saprophyte it has no particular resemblance to *Scl. Libertiana* under the same conditions, producing much less mycelium and a great abundance of conidia. When growing as a parasite it is in some respects indistinguishable from the other species. The mycelium is entirely similar and organs of attachment are produced which are likewise exactly the same. The effect upon the plant is often entirely similar. As a parasite it appears to produce fewer conidia in proportion to the degree of parasitism. Often in newly affected tissue none appear. Sclerotia are often produced in cultures and on affected plants but with considerable uncertainty. Not rarely cultures made from conidia produce no spores whatever, but numerous sclerotia. This is most common when parasitic material is used. The sclerotia are highly characteristic and suffice at all times to distinguish this species from the other. They usually have a narrow form, especially in tube cultures, and are always thin and inseparably attached to the substratum, lacking entirely the definite form and the solid, "meaty" structure of the sclerotia of *Scl. Libertiana*. So far as known no Peziza has ever

been obtained from sclerotia developed from *Botrytis*. On the basis of internal structure these sclerotia cannot be clearly distinguished from the others. They vary in compactness and seem to have no very characteristic makeup. The two species often occur together, as Botrytis does in connection with many other fungi, and it is believed that the only unprejudiced argument which has ever existed in favor of the connection between *Sclerotinia Libertiana* and *Botrytis cinerea* is their frequent simultaneous occurrence, in connection with the similarity of the mycelium and the fact that they often attack plants in a very similar manner; all of which is explained by their close relationship. When carried further than this they may be readily separated and distinguished from one another and the distinctive characters brought out which have been described.

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EXPLANATION OF PLATES XXV–XXVII.

PLATE XXV.

FIG. 1. Typical conidiophore of *Botrytis cinerea* Pers.

FIG. 2. Portion of same, more enlarged.

FIG. 3. Conidiophore from old, exhausted culture.

FIG. 4. Botrytis slightly enlarged.

FIGS. 5–9. Botrytis from onion.

FIGS. 10–11. Conidia of *Botrytis cinerea*.

FIG. 12. Conidia of Botrytis from onion.

FIGS. 13–17. Development of conidiophore of *Botrytis cinerea* from mycelium within a plant.

FIG. 18. Development of terminal branches.

FIGS. 19–22. Forms of organs of attachment.

PLATE XXVI.

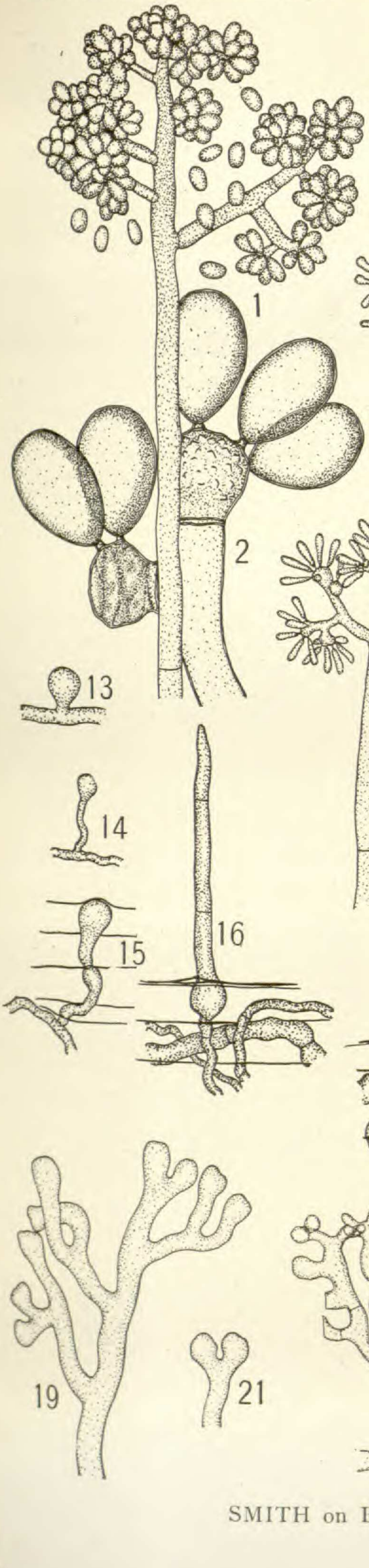
FIGS. 23–25. Forms of organs of attachment.

FIG. 26. Tip of a branch of an organ of attachment growing against glass.

FIG. 27. Mycelium of Botrytis from stem of lettuce seedling, causing "damping off."

FIG. 28. Cross connections in Botrytis mycelium.

FIG. 29. Filaments of *Sclerotinia Libertiana* Fckl., entering lettuce leaf.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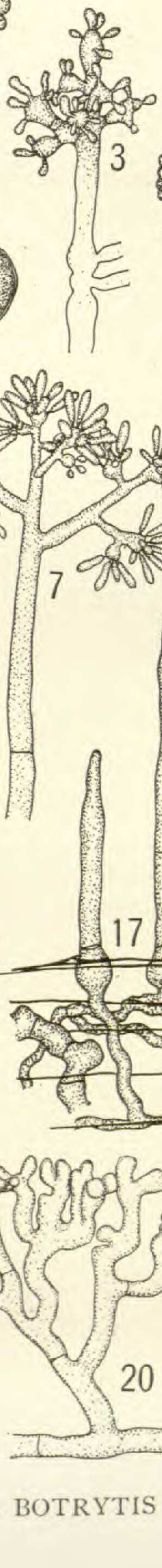
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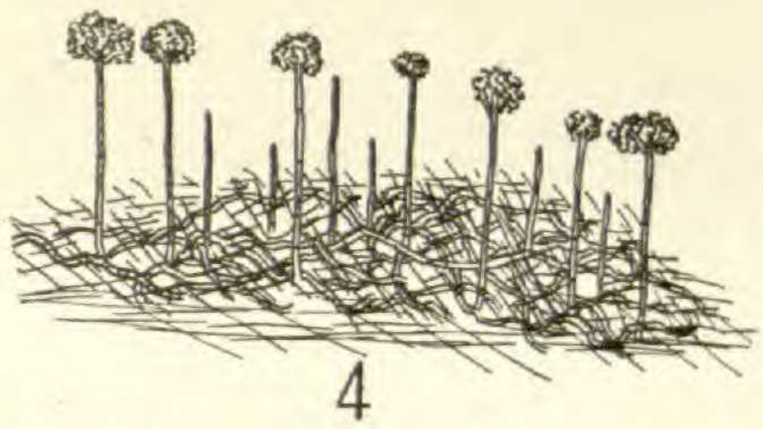
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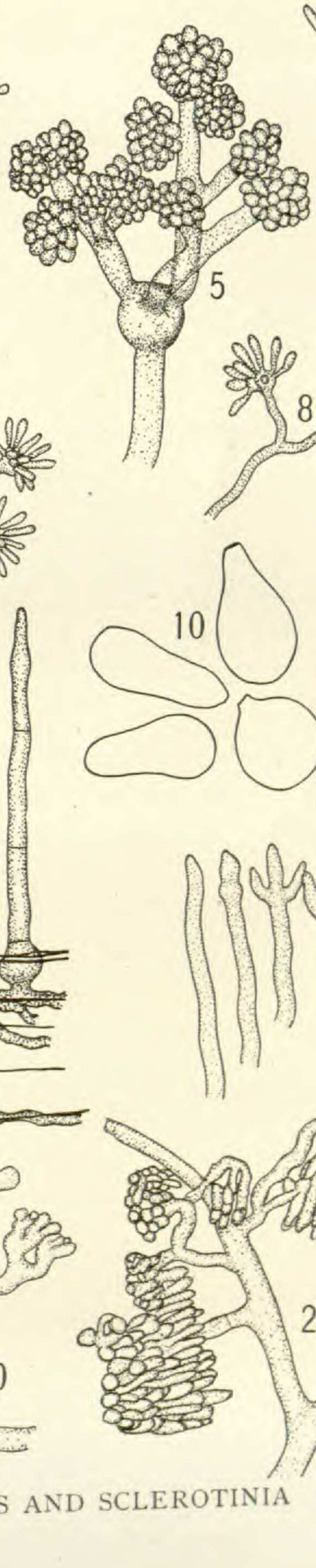
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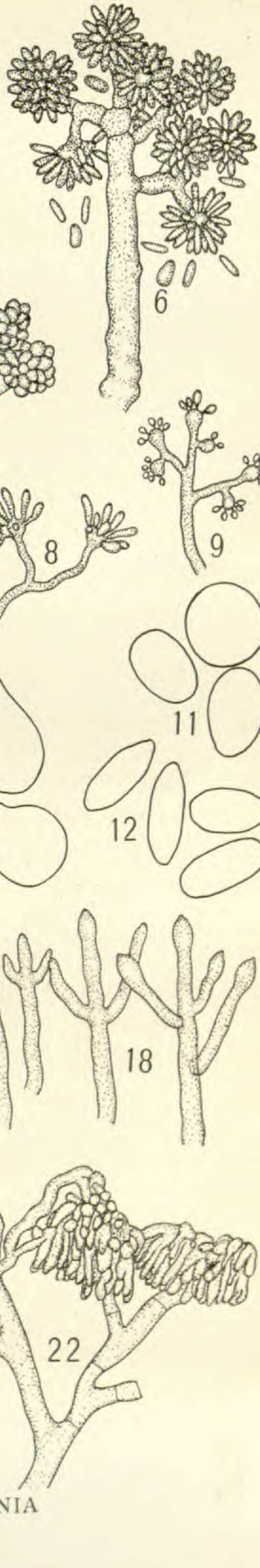
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SMITH on BOTRYTIS AND SCLEROTINIA